Effects of Turbidity and Cover on Prey Selectivity of Adult Smallmouth Bass

MARK W. CARTER*1

Illinois Natural History Survey, Kaskaskia Biological Station, Rural Route 1, Box 157, Sullivan, Illinois 61951, USA; and Department of Natural Resources and Environmental Sciences, University of Illinois Urbana–Champaign, Champaign, Illinois 61820, USA

DANIEL E. SHOUP²

Illinois Natural History Survey, Kaskaskia Biological Station, Rural Route 1, Box 157, Sullivan, Illinois 61951, USA

JOHN M. DETTMERS³

Department of Natural Resources and Environmental Sciences, University of Illinois Urbana–Champaign, Champaign, Illinois 61820, USA

DAVID H. WAHL

Illinois Natural History Survey, Kaskaskia Biological Station, Rural Route 1, Box 157, Sullivan, Illinois 61951, USA; and Department of Natural Resources and Environmental Sciences, University of Illinois Urbana–Champaign, Champaign, Illinois 61820, USA

Abstract.—Environmental factors such as turbidity and habitat complexity affect many aspects of aquatic food webs, including predator–prey interactions. We examined the effects of turbidity (0, 5, 10, 20, 40 nephelometric turbidity units [NTU]) and cover (presence or absence) on prey selection by adult smallmouth bass *Micropterus dolomieu* (mean \pm SD = 290 \pm 41 mm total length) in laboratory pools. Individual predators were given a choice of five northern crayfish *Orconectes virilis*, five golden shiners *Notemigonus crysoleucas* (a pelagic fish), or five round goby *Neogobius melanostomus* (an invasive benthic fish). Smallmouth bass selected round goby at low turbidities (0 and 5 NTU) and golden shiners at the highest turbidity (40 NTU) in trials without cover. With cover, smallmouth bass increased selectivity for golden shiners, particularly at the turbidity extremes (0, 20, and 40 NTU). Northern crayfish were negatively or neutrally selected in all trials across both turbidity and cover treatments. Turbidity had a greater effect than cover on prey consumption rate, which decreased as turbidity increased. Our results suggest that turbidity and cover, two important environmental variables, can influence prey selectivity by smallmouth bass.

Predation is an important structuring force for communities in a variety of systems (Connell 1975). This is certainly true for fishes and their prey because population densities (Hixon and Carr 1997) and size structures (Broenmark et al. 1995) of prey can be affected, with results cascading to lower trophic levels (Carpenter and Kitchell 1985). Thus, predator–prey interactions have been studied extensively by aquatic ecologists. Such research has concluded that the outcomes of predator–prey interactions depend on the behaviors of both predators and prey. Fish predators make decisions about where, when, and how to feed (Dill 1983) to optimize foraging success, whereas prey use any number of behaviors to avoid predation (see Endler 1986). Foraging decisions of predators (Dill 1983) and antipredator behaviors of prey (Savino and Stein 1982; Miner and Stein 1996; Shoup et al. 2003) also change with differences in environmental factors, such as water clarity, water temperature, and availability of complex habitat.

The effects of environmental variables such as turbidity on interactions between fish predators and their prey have been repeatedly demonstrated. Turbidity levels can be highly variable due to seasonal changes in suspended sediments and algal blooms as well as wind-driven suspension of sediments (Abrahams and Kattenfeld 1997). In streams, sudden changes in water levels can cause extreme changes in turbidity (Larimore 1975), as can strong wind events in lakes with large fetches. As turbidity increases, both

^{*}Corresponding author: mark.carter@ferc.gov

¹Present address: Federal Energy Regulatory Commission, Washington, D.C., USA.

²Present address: Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, Oklahoma, USA.

³Present address: Great Lakes Fishery Commission, Ann Arbor, Michigan, USA.

Received August 4, 2008; accepted September 6, 2009 Published online December 31, 2009

predators and prey experience reduced encounter rates (Gregory and Levings 1996) and predator search time is increased (Meager et al. 2005). Foraging success generally decreases with increasing turbidity (Vandenbyllaardt et al. 1991; Gregory and Levings 1998; Rowe and Dean 1998); prey may perceive less predation risk and thus reduce antipredator behavior as turbidity increases (Gregory 1993; Miner and Stein 1996; Abrahams and Kattenfeld 1997). Reaction distances of both predators (Vinyard and O'Brien 1976; Barrett et al. 1992; Sweka and Hartman 2003) and prey (Miner and Stein 1996) decrease as turbidity increases.

Most previous studies of the effects of turbidity have examined planktivorous predators and relatively nonmobile prey. Predator-prey interactions differ between piscivorous and planktivorous fishes in many aspects (see review by Breck 1993), but these differences are mainly due to such factors as prey size, mobility, and contrast (Asknes and Utne 1997). One obvious difference is the increased ability of the prey of piscivores to escape detection and capture (Gill 2003). In clear water, piscivores can detect prey at greater distances than planktivores can detect zooplankton (Breck 1993), so the capacity of turbidity to reduce detection of prey could affect piscivores more than planktivores (De Robertis et al. 2003). Whether differences in prey detection caused by turbidity can alter selectivity by a predator when presented with various prey species is unknown.

The presence of cover is another environmental variable that can alter predator-prey dynamics (Diehl 1992). Like turbidity, the presence of cover reduces predation rates simply because visual encounters between predators and prey are reduced (Crowder and Cooper 1979). Thus, predators often switch foraging strategies with changes in habitat complexity (Savino and Stein 1982). Predatory success generally decreases with increasing habitat complexity (Gregory and Levings 1996; Ostrand et al. 2004; Gadomski et al. 2005), but this can differ by species (Savino and Stein 1989; Christenssen and Persson 1993; Wahl 1995). Prey can alter antipredator behaviors to more easily escape predation when cover is available (Miner and Stein 1996). Changes in prey selectivity by piscivorous fishes in two-prey systems as habitat complexity increases have been demonstrated for both largemouth bass Micropterus salmoides (Schramm and Zale 1985) and European perch Perca fluviatilis (Christenssen and Persson 1993).

We used piscivorous smallmouth bass *M. dolomieu* to test the effects of turbidity and presence of cover on selectivity among three morphologically different prey species with varying antipredator defenses. Smallmouth bass generally inhabit clear water; they can

experience reduced stomach fullness (Easton et al. 1996) and decreased reaction distance to prey (Sweka and Hartman 2003) as turbidity increases. The goal of this study was to test the hypotheses that increasing turbidity and the presence of cover alter prey selectivity of a piscivorous fish.

Methods

The round goby *Neogobius melanostomus*, an invasive benthic fish; northern crayfish *Orconectes virilis*, a benthic invertebrate; and golden shiner *Notemigonus crysoleucas*, a schooling pelagic fish, were chosen because they represent common prey types for smallmouth bass (Tester 1932; Lewis and Helms 1964; Steinhart et al. 2004). The round goby was chosen as prey because of the recent concern caused by its invasion of the Great Lakes region (Jude et al. 1992) and because round goby are now an established component of smallmouth bass diets (Steinhart et al. 2004; S. Creque, Illinois Natural History Survey [INHS], unpublished data).

Smallmouth bass were collected from local lakes and rivers in Illinois by electrofishing. Northern crayfish were seined from ponds at the Sam Parr Biological Station, Kinmundy, Illinois. Golden shiners were purchased from a local bait dealer, and round goby were seined from Illinois harbors of Lake Michigan. Predators and prey were held indoors at the Kaskaskia Biological Station, Sullivan, Illinois, and were allowed to acclimate at least 2 weeks before trials were conducted. During this time, smallmouth bass were fed each of the three prey types to ensure that the predators had experience consuming these prey before experiments. The choice of prey sizes is inherently complex because length, girth, volume, energy density, and handling time often do not scale together across morphologically different prey types. Comparison of fish and crayfish is problematic because the standard measurements (total length [TL] or carapace length) for crayfish do not account for the size of their chelae or their tail region. To avoid such difficulties, we used previously published optimal prey sizes that accounted for the energy density (dry mass) and handling time associated with each prey type. Target optimal prey sizes were 12-19% of predator TL (Stein 1977) for northern crayfish and 20–30% of predator TL for round goby and golden shiners (Winemiller and Taylor 1987). The actual sizes (TL) of northern crayfish (mean \pm SD = 44 \pm 0.01 mm), golden shiners (70 \pm 0.01 mm), and round goby (68 \pm 0.01 mm) used in this experiment were within the target ranges for the sizes of smallmouth bass used (mean \pm SD = 290 \pm 41 mm; range = 230-355 mm).

Trials were conducted indoors using round alumi-

num tanks (67-cm depth; 1.8-m diameter; 1,600-L total volume). Water temperature was held between 18°C and 19°C, and photoperiod was set at 12 h light : 12 h dark. Predators were starved for 24 h before each trial to standardize hunger levels (Gardner 1981). Mean duration of trials varied from 3.5 to 42.6 h depending on variation in feeding rates among individuals and turbidity levels (Table 1). Each individual predator (N = 15) was exposed to prey at each of five turbidity levels (0, 5, 10, 20, or 40 nephelometric turbidity units [NTU]) and two levels of cover (presence or absence). Order of treatment combinations was randomly assigned such that each predator was tested once at each treatment combination (i.e., N = 10 trials/ predator). Bentonite clay and water were vigorously stirred to produce a slurry that was added to achieve the desired turbidity levels. Turbidity treatment conditions were maintained by a 15-cm air stone suspended in each tank. Turbidity (NTU) was measured using a LaMotte Model 2020 turbidimeter. Turbidity levels were checked 1-5 times/trial depending on trial duration, and levels were adjusted by adding the turbidity slurry as needed. Variation within 10% of the treatment level was considered acceptable. Mean turbidity levels were within 1 NTU of the target treatment level (Table 1). Secchi depth was recorded for reference purposes just prior to the start of each trial because NTU measurements, although very precise, can vary widely among turbidity meters and water bodies, whereas Secchi depth has more immediate environmental relevance (see review by Davies-Colley and Smith 2001). Simulated cover consisted of ten 5cm lengths of 10-cm-diameter polyvinyl chloride pipe cut in half along the diameter, which were placed haphazardly on the bottom of the tank.

Five individuals representing each of the three prey types were placed in each tank and allowed to acclimate for 30 min before the predator was added to the tank. This prey density (5.9 fish/m^2) was chosen because it fell within the range of densities used in previous feeding experiments (Savino and Stein 1982; Wahl and Stein 1988) and is similar to the range of field-determined densities for these prey types (Momot et al. 1978; Mittlebach et al. 1995; Wray and Corkum 2001). Trials ended when at least one prey item was consumed. Additional prey were occasionally consumed (typically one or two but never more than four individuals). At the end of a trial, the tank was drained, the predator was removed from the tank, and the remaining prey were counted. If no prey or more than four prey were consumed, the trial was excluded from analysis and was run again to ensure that selectivity could be calculated and to avoid drastically changing prey densities as prey were consumed. Two predators

TABLE 1.—Mean and SE of turbidity level (nephelometric turbidity units [NTU], mean per trial) and duration (h) of laboratory experiments conducted to examine prey selectivity by smallmouth bass presented with three different prey types.

Targeted treatment level (NTU)	Actual turbidity (NTU)		Trial duration (h)	
	Mean	SE	Mean	SE
0	0.56	0.07	3.5	0.8
5	5.58	0.13	15.7	3.6
10	10.98	0.25	23.3	3.9
20	20.91	0.31	29.8	3.3
40	41.19	0.60	42.6	5.0

completed only nine trials each: one of these fish died before completing the trial at 20 NTU without cover, and the second fish would not eat after multiple attempts at 40 NTU without cover. Thus, 148 trials were conducted with 15 smallmouth bass.

Prey selectivity was determined using Chesson's alpha values for each prey species at each treatment combination (see equation in Chesson 1983 assuming nonreplacement of consumed prey during the trial). Mean Chesson's alpha values and 95% confidence intervals were calculated for each prey type and treatment combination using a least-squares means multiple comparison test (MIXED procedure in the Statistical Analysis System [SAS] version 8.2; SAS Institute, Inc., Cary, North Carolina). Confidence intervals for Chesson's alpha values were compared against random feeding (1 divided by the number of prey types) to assess selectivity; intervals entirely above the random feeding line were interpreted as positive selection for a particular prey, overlapping intervals were interpreted as neutral selection, and intervals entirely below the random feeding line were interpreted as negative selection (Graeb et al. 2005; Rudershausen et al. 2005). To examine whether consistent linear increases in selectivity occurred with increasing turbidity and to account for repeated measurements taken on each predator, we applied repeated-measures linear regressions (MIXED procedure in SAS) on treatment level (NTU) against Chesson's alpha values for each of the three prey types both with and without cover. A Bonferroni adjustment was used to account for multiple individual regressions, and the significance level was therefore set at 0.008. The slopes of these regressions were compared with zero to test for positive or negative linear trends in feeding selectivity with increasing turbidity.

Number of prey consumed per hour was analyzed using analysis of variance (ANOVA; MIXED procedure in SAS) to test for differences attributed to turbidity and cover. If the ANOVA indicated differ-

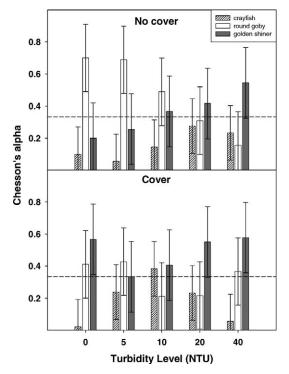


FIGURE 1.—Mean ($\pm 95\%$ confidence interval [CI]) Chesson's alpha in trials without cover (top panel) and with cover (bottom panel) across five turbidity treatments (NTU = nephelometric turbidity units). Selectivity by smallmouth bass is presented for three prey types: northern crayfish (hatched bars), round goby (open bars), and golden shiners (dark shaded bars). Selection was assessed by overlap between 95% CIs and the dashed neutral selection line (1/number of prey species tested).

ences, they were parsed among treatments using a least-squares means multiple comparison test with a Tukey–Kramer adjustment. Pearson's product-moment correlation coefficient (CORR procedure in SAS) was also calculated to test for correlation between the number of prey consumed per hour and turbidity.

Results

A power function related turbidity (NTU) to Secchi depth (cm): Secchi depth = $129 \times \text{NTU}^{-0.045}$ ($r^2 = 0.94$). For these experiments, Secchi depth for each treatment was 62.5 cm for 5 NTU; 45.8 cm for 10 NTU; 33.5 cm for 20 NTU; and 24.5 cm for 40 NTU. Secchi depth for the 0-NTU treatment was not measurable because water clarity exceeded the depth of the tank.

Selectivity by smallmouth bass differed with both turbidity and cover (Figure 1). The effects of turbidity and cover on prey selectivity also differed among the

TABLE 2.—Results of linear regression analyses testing the effect of turbidity on prey selection (Chesson's alpha) by smallmouth bass presented with three potential prey species in the presence or absence of cover. Slopes significantly different than zero (P < 0.008) are indicated by asterisks.

		•		
Species	Intercept	Slope	Р	R^2
	No	cover		
Northern crayfish	0.02	0.005	0.15	0.04
Round goby	0.69	-0.01*	0.0001*	0.19
Golden shiner	0.20	0.01*	0.003*	0.09
	Co	over		
Northern crayfish	0.09	0.0001	0.87	0.006
Round goby	0.36	-0.002	0.65	0.002
Golden shiner	0.40	0.005	0.20	0.01

three prey types. Northern crayfish were negatively or neutrally selected in all treatments. Selection for northern crayfish changed from negative to neutral with increasing turbidity in trials without cover (Figure 1). In trials with cover, northern crayfish were neutrally selected at 5-, 10-, and 20-NTU treatments but were negatively selected at 0 and 40 NTU. Selectivity for northern crayfish did not change linearly (Table 2) with turbidity in trials without cover (F = 2.4, df = 14, P =0.15) or in trials with cover (F = 0.03, df = 14, P =0.90).

Selectivity for round goby in trials without cover was positive at turbidities below 10 NTU but declined to neutral at 10 NTU and higher turbidities. Regression analyses showed that selectivity for round goby decreased linearly (F = 27.8, df = 14, P = 0.0001) with increasing turbidity (Table 2). With cover added, selectivity for round goby was neutral across all turbidity levels. Regression analyses found no linear selectivity pattern for round goby in trials with cover (F = 0.2, df = 14, P = 0.70).

Golden shiners were consumed in the same proportion at which they were available in the environment across turbidity levels in trials without cover, but selectivity was marginally positive at 40 NTU. Although selectivity for golden shiners did not statistically increase across treatments, selectivity did increase linearly with increasing turbidity (F = 12.8, df = 14, P = 0.003). With cover added, selectivity was neutral at medium (5 and 10 NTU) turbidity levels but was positive in the 0-, 20-, and 40-NTU treatments. In trials with cover, regression analyses did not indicate a linear change in selectivity with turbidity for golden shiners (F = 1.8, df = 14, P = 0.20).

Number of prey consumed per hour by smallmouth bass differed with turbidity (F = 10.6; df = 4, 71; P < 0.01). In contrast, it did not differ with presence or absence of cover (F = 0.7; df = 1, 71; P = 0.40). The turbidity \times cover interaction term was also not

significant (F = 0.08; df = 4, 71; P = 0.99). Thus, trials with and without cover were combined to assess the number of prey consumed per hour across turbidities. Consumption rate at 0 NTU was higher than at all other turbidity levels (t = 5.9-7.2, df = 70, all P < 0.01; Figure 2). Number of prey consumed per hour did not differ between the 5-, 10-, 20-, and 40-NTU treatments (t = 0.1-1.4, df = 70, all P > 0.70), but a correlation revealed a negative relationship between turbidity and feeding rate (r = -0.3, P < 0.01).

Discussion

Our results provide evidence that turbidity affects the patterns of prey selectivity by smallmouth bass. In clear water without cover, round goby were selected over golden shiners, whereas northern crayfish were avoided. As turbidity increased, smallmouth bass switched from selecting round goby and avoiding northern crayfish in clear water to neutrally selecting each of the three prey species in more turbid water. Regression analyses showed that selection increased for golden shiners and decreased for round goby with increasing turbidity in trials without cover. One explanation for these selection patterns is that turbidity reduces the amount of light available in the water column; these reductions increase exponentially with depth (Kirk 1985). Because golden shiners are pelagic schooling fish, individuals may have inhabited an area higher in the water column (Einfalt and Wahl 1997), where more light was available relative to areas inhabited by the other two prey types. In our experiments, golden shiners were frequently observed swimming in schools near the surface in both turbid and clear water. An alternative explanation is that golden shiners successfully avoid predators in clear water (Einfalt and Wahl 1997), but this success decreases relative to other prey when turbidity increases. Increasing turbidity reduces the cohesiveness and increases the activity rates of minnow schools (Vandenbyllaardt et al. 1991) as well as weakens prey startle responses (Gregory 1993). We cannot be certain whether patterns we observed are due to predator or prey behaviors because the turbid water prevented observation of fish behavior.

In addition to turbidity, the presence of cover also affected smallmouth bass selectivity among the prey species. Golden shiners were positively selected in clear (0 NTU) and turbid (40 NTU) water. Neutral selection occurred for round goby and northern crayfish across turbidity levels and for golden shiners at intermediate turbidities (5 and 10 NTU). Turbidity at the level of 20 NTU represented a transition for selection of golden shiners. These patterns of no consistent linear trends with increasing turbidity in

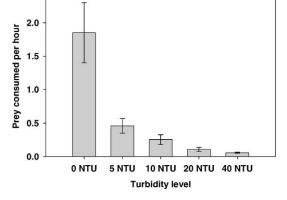


FIGURE 2.—Mean (\pm SE) number of prey consumed per hour by smallmouth bass at five turbidity levels (NTU = nephelometric turbidity units; trials with and without cover are combined) in a laboratory tank experiment.

trials with cover were supported by regression analyses. Both round goby (Jude et al. 1992) and crayfish (Dorn and Mittelbach 1999) use cover to avoid predation, whereas golden shiners do not (Boyd and Parsons 1998); thus, it is possible that the presence of cover provided refuge only for the two benthic species, causing predator selection for golden shiners at low and high turbidities. In previous studies, round goby (Belanger and Corkum 2003) and crayfish (Stein and Magnuson 1976) each experienced reduced predation when cover was present. Although such behavior was impossible to quantify because of turbidity, round goby and northern crayfish were often observed using cover when tanks were drained.

Although this study was not designed to directly test feeding rate (i.e., trial duration varied with treatment to ensure that only one or two prey were consumed in each trial), we calculated the mean number of prey consumed per hour for each trial as a measure of food consumption rate. Our experiment was not designed to test the long-term effects of turbidity on predator feeding rate because all of the animals were maintained in clear water. We believe that these results do, however, provide insight into the effects of short-term turbidity pulses (caused by flooding, wind, upwelling, etc.) on foraging return for visual predators. Our feeding selectivity results could be biased because animals were maintained in clear water, but we believe that they yield useful ecological data about the capacity of turbidity to affect prey selection by visually foraging fishes.

The reduced number of prey consumed per hour with increasing turbidity indicates that smallmouth bass easily capture prey in clear water but have more difficulty as water becomes even slightly more turbid. Our results suggest that visually feeding piscivores will have difficulty foraging for up to 2 d immediately after a turbidity pulse. These results differ from those obtained with largemouth bass (a congener of the smallmouth bass), for which the number of prey captured was not different among 1-37-NTU treatments in the field (Reid et al. 1999). In the laboratory, however, largemouth bass have shown more difficulty foraging in more turbid water (Shoup and Wahl 2009). Generally, tolerance for turbid water is higher in largemouth bass than in smallmouth bass (Winemiller and Taylor 1987), and largemouth bass are more likely to successfully forage in turbid water than are smallmouth bass. The reduced consumption by smallmouth bass with increased turbidity is, however, similar to results for piscivorous walleyes Sander vitreus (Vandenbyllaardt et al. 1991), a variety of other piscivores (Gregory and Levings 1998), and many other invertivorous and planktivorous species (Rowe and Dean 1998).

Increased turbidity significantly decreased the number of prey consumed per hour, whereas the presence of cover had no effect, suggesting that turbidity is more important than cover in influencing smallmouth bass consumption of prey. Previous research indicates that increased vegetation or complex habitat generally results in decreased predatory success (Savino and Stein 1989; Ostrand et al. 2004). Our results suggest that the presence of cover affected which prey were chosen but not the rate at which prey were eaten. A threshold may exist for the level of habitat complexity required before major changes in consumption rates occur (Gotceitas and Colgan 1989). The amount of cover in our study may not have exceeded such a threshold; however, we do not believe this to be the case because sufficient structure was provided for each individual prev expected to use the cover. In addition to the quantity of cover, the type of cover also affects predator-prey dynamics (Christenssen and Persson 1993). Previous studies that assessed habitat complexity and predatory success used largemouth bass and bluegills Lepomis macrochirus with varying levels of vegetation (Savino and Stein 1982, 1989; Gotceitas and Colgan 1989), which was different in type than the simulated benthic cover used in our study. Thus, it is possible that bottom structure used by benthic prey affects predator-prey dynamics differently than vertical structure used by littoral species.

The negative and neutral selection of northern crayfish across all treatment combinations was unexpected. Multiple studies demonstrated that crayfish dominate the diet of smallmouth bass (Tester 1932; Probst et al. 1984; Dorn and Mittelbach 1999; Weidel et al. 2000). Seasonal shifts (Clady 1974; Danehy and

Ringler 1991; Gilliland et al. 1991) and ontogenetic shifts (Dorn and Mittelbach 1999; Weidel et al. 2000) between crayfish and other prey have been described, but cravfish are generally recognized as a preferred prey taxon for adult smallmouth bass. Another recent study of smallmouth bass prey selectivity in clear water found that these predators preferred round goby to emerald shiners Notropis atherinoides and that crayfish were consumed least (Kim 2007). Our use of optimalsized prey (Stein 1977; Winemiller and Taylor 1987) accounts for energetic differences among round goby (3.65 kJ/g wet mass; Kim 2007), emerald shiners (5.14 kJ/g wet mass; Bryan et al. 1996), and crayfish (3.12 kJ/g wet mass; Kelso 1973). The low energetic gain derived from consuming crayfish contrasts with the near-ubiquity of crayfish in field diets of smallmouth bass. Similarly, round goby, which are lower in energy relative to other fishes, were preferred by young smallmouth bass when the two species co-occurred in nearshore habitats of Lake Erie (Steinhart et al. 2004), highlighting the importance of prey availability in determining which prey are consumed. The results of Kim (2007), in combination with our results, suggest that smallmouth bass do not prefer crayfish more than other prey types but crayfish may be the most common prey species in the habitats frequented by smallmouth bass. Graeb et al. (2005) described the yellow perch P. flavescens as a generalist predator that selected prey passively based on encounter rates and foraging efficiency in comparison with the walleye, a specialist piscivore that actively selected fish prey to maximize growth. Smallmouth bass have long been recognized as opportunistic feeders (Coble 1975) because certain adult populations consume zooplankton (Dunsmoor et al. 1991) and hatching insects (Clady 1974) when abundance of such invertebrates is high and when fish or crayfish prey are not available. Disparity with field diet data is probably due to differences in encounter rates, foraging efficiency, or both rather than to differing preferences; thus, smallmouth bass should be considered generalist predators.

The findings of (1) decreasing selectivity by smallmouth bass for a benthic fish and increasing selectivity for a pelagic fish as water became turbid and (2) greater selectivity for a pelagic fish when cover was present than when cover was absent demonstrate the ability of key environmental variables such as turbidity and habitat complexity to alter outcomes of predator-prey interactions. Not only did these environmental variables affect the number of prey consumed per hour, they also altered the piscivores' selection of prey species. Similar turbidity-induced changes in diet have been observed for piscivorous largemouth bass (Shoup and Wahl 2009) and skipjack *Elops machnata* (Hecht

and Van der Lingen 1992). Turbidity may also cause changes in prey selection by planktivores given the well-documented ability of turbidity to alter planktivores' reaction distances, rates of prey encounter, and predation rates (Vinyard and O'Brien 1976; Vandenbyllaardt et al. 1991; Gregory and Levings 1996; Miner and Stein 1996); however, the effect of turbidity on selection by planktivores has not been directly tested. Such changes in the outcome of predator-prey interactions may translate to altered food web structure across aquatic communities with changing habitat (i.e., turbidity, cover) characteristics. Thus, environmental heterogeneity must be accounted for in ecological studies, specifically those dealing with predictions related to piscivore-prey relationships and the implications for food web interactions.

Acknowledgments

We thank L. Einfalt for help maintaining experimental fish at the INHS Kaskaskia Biological Station. M. Weber and staff at the Lake Michigan Biological Station and Sam Parr Biological Station helped collect fish. The comments of two anonymous reviewers substantially improved this manuscript. Funding for this project was partially provided by a grant from the Illinois Smallmouth Alliance and from the R. Weldon Larimore Research Grant administered by the INHS. Additional support was provided by the INHS and the Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana-Champaign.

References

- Abrahams, M., and M. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40:169–174.
- Asknes, D. L., and A. C. W. Utne. 1997. A revised model of visual range in fish. Sarsia 82:137–147.
- Barrett, J. C., G. D. Grossman, and J. Rosenfeld. 1992. Turbidity-induced changes in reactive distance of rainbow trout. Transactions of the American Fisheries Society 121:437–443.
- Belanger, R. M., and L. D. Corkum. 2003. Susceptibility of tethered round gobies (*Neogobius melanostomus*) to predation in habitats with and without shelters. Journal of Great Lakes Research 29:588–593.
- Boyd, G. L., and B. R. Parsons. 1998. Swimming performance and behavior of golden shiner, *Notemigonus crysoleucas*, while schooling. Copeia 2:467–471.
- Breck, J. E. 1993. Foraging theory and piscivorous fish: are forage fish just big zooplankton? Transactions of the American Fisheries Society 122:902–911.
- Broenmark, C., C. A. Paszkowski, W. M. Tonn, and A. Hargeby. 1995. Predation as a determinant of size structure in populations of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*). Ecology of Freshwater Fish 4:85–92.

- Bryan, S. D., C. A. Soupier, W. G. Duffy, and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. Journal of Freshwater Ecology 11:153–161.
- Carpenter, S. R., and J. F. Kitchell. 1985. Cascading trophic interactions and lake productivity. Bioscience 35:634– 639.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.
- Christenssen, B., and L. Persson. 1993. Species-specific antipredatory behaviours: effects of prey choice in different habitats. Behavioral Ecology and Sociobiology 32:1–9.
- Clady, M. D. 1974. Food habits of yellow perch, smallmouth bass, and largemouth bass in two unproductive lakes in northern Michigan. American Midland Naturalist 91:453–459.
- Coble, D. W. 1975. Smallmouth bass. Pages 21–33 in R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts.
- Crowder, L. B., and W. E. Cooper. 1979. Habitat structural complexity and the interaction between bluegill and their prey. Ecology 63:1802–1813.
- Danehy, R. J., and N. H. Ringler. 1991. Ecology of smallmouth bass in the nearshore of Mexico Bay, Lake Ontario. Pages 66–72 in D. C. Jackson, editor. The first international smallmouth bass symposium. Mississippi State University, Mississippi State.
- Davies-Colley, R. J., and D. G. Smith. 2001. Turbidity, suspended sediment, and water clarity: a review. Journal of the American Water Resources Association 37:1085– 1101.
- De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences 60:1517–1526.
- Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646–1661.
- Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Sciences 40:398–408.
- Dorn, N. J., and G. G. Mittelbach. 1999. More than predator and prey: a review of interactions between fish and crayfish. Vie et Milieu 49:229–237.
- Dunsmoor, L. K., D. H. Bennett, and J. A. Chandler. 1991. Prey selectivity and growth of a planktivorous population of smallmouth bass in an Idaho reservoir. Pages 14–23 *in* D. C. Jackson, editor. The first international smallmouth bass symposium. Mississippi State University, Mississippi State.
- Easton, R. S., D. J. Orth, and J. R. Voshell. 1996. Spatial and annual variation in the diets of smallmouth bass, *Micropterus dolomieu*. Environmental Biology of Fishes 46:383–392.
- Einfalt, L. M., and D. H. Wahl. 1997. Prey selection by

juvenile walleye as influenced by prey morphology and behavior. Canadian Journal of Fisheries and Aquatic Sciences 54:2618–2626.

- Endler, J. A. 1986. Defense against predators. Pages 109–134 in M. E. Feder and G. V. Lauder, editors. Predator-prey relationships. University of Chicago Press, Chicago.
- Gadomski, D. M., and M. J. Parsley. 2005. Effects of turbidity, light level, and cover on predation of white sturgeon larvae by prickly sculpins. Transactions of the American Fisheries Society 134:369–374.
- Gardner, M. B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. Ecology 62: 571–578.
- Gill, A. B. 2003. The dynamics of prey choice in fish: the importance of prey size and satiation. Journal of Fish Biology 63:105–116.
- Gilliland, E., R. Horton, B. Hysmith, and J. Moczygemba. 1991. Smallmouth bass in Lake Texoma: a case history. Pages 136–142 in D. C. Jackson, editor. The first international smallmouth bass symposium. Mississippi State University, Mississippi State.
- Gotceitas, V., and P. Colgan. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80:158–166.
- Graeb, B. D. S., T. Galarowicz, D. H. Wahl, J. M. Dettmers, and M. J. Simpson. 2005. Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. Canadian Journal of Fisheries and Aquatic Sciences 62:2010–2020.
- Gregory, R. S. 1993. The effect of turbidity on the predator avoidance behaviour of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50:241–246.
- Gregory, R. S., and C. D. Levings. 1996. The effects of turbidity and vegetation on the risk of juvenile salmonids, *Oncorhynchus* spp., to predation by adult cutthroat trout *O. clarki*. Environmental Biology of Fishes 47:279–288.
- Gregory, R. S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127:275–285.
- Hecht, T., and C. D. Van der Lingen. 1992. Turbidity-induced changes in feeding strategies of fish in estuaries. South African Journal of Zoology 27:95–107.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946–949.
- Jude, D. J., R. H. Reider, and G. R. Smith. 1992. Establishment of Gobiidae in the Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences 49:416–421.
- Kelso, J. R. M. 1973. Seasonal energy changes in walleye and their diet in West Blue Lake, Manitoba. Transactions of the American Fisheries Society 102:363–368.
- Kim, G. W. 2007. How benthic-pelagic coupling by fish affects fate of contaminants, nutrients, and energy. Doctoral dissertation. Ohio State University, Columbus.
- Kirk, J. T. 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. Hydrobiologia 125:195–208.
- Larimore, R. W. 1975. Visual and tactile orientation of smallmouth bass fry under floodwater conditions. Pages

323–332 *in* H. J. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

- Lewis, W. M., and D. R. Helms. 1964. Vulnerability of forage organisms to largemouth bass. Transactions of the American Fisheries Society 93:315–318.
- Meager, J. J., T. Solbakken, A. C. Utne-Palm, and T. Oen. 2005. Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62:1978–1984.
- Mittlebach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: A long-term, whole-lake study of predator extinction and reintroduction. Ecology 76:2347–2360.
- Miner, J. G., and R. A. Stein. 1996. Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. Transactions of the American Fisheries Society 125:97–103.
- Momot, W. T., H. Gowing, and P. D. Jones. 1978. The dynamics of crayfish and their role in ecosystems. American Midland Naturalist 99:10–35.
- Ostrand, K. G., B. J. Braeutigam, and D. H. Wahl. 2004. Consequences of vegetation density and prey species on spotted gar foraging. Transactions of the American Fisheries Society 133:794–800.
- Probst, W. E., C. F. Rabeni, W. G. Covington, and R. E. Marteney. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. Transactions of the American Fisheries Society 113:283–294.
- Reid, S. M., M. G. Fox, and T. H. Whillans. 1999. Influence of turbidity on piscivory in largemouth bass (*Micropterus* salmoides). Canadian Journal of Fisheries and Aquatic Sciences 56:1362–1369.
- Rowe, D. K., and T. L. Dean. 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. New Zealand Journal of Marine and Freshwater Research 32:21–29.
- Rudershausen, P. J., J. E. Tuomikoski, J. A. Buckel, and J. E. Hightower. 2005. Prey selectivity and diet of striped bass in western Albemarle Sound, North Carolina. Transactions of the American Fisheries Society 134:1059–1074.
- Santucci, V. J. Jr., and D. H. Wahl. 2003. The effects of growth, predation, and first-winter mortality on recruitment of bluegill cohorts. Transactions of the American Fisheries Society 132:346–360.
- Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegill as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111:255–266.
- Savino, J. F., and R. A. Stein. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. Animal Behaviour 37:311–321.
- Schramm, H. L., and A. V. Zale. 1985. Effects of cover and prey size on preferences of juvenile largemouth bass for blue tilapias and bluegills in tanks. Transactions of the American Fisheries Society 114:725–731.
- Shoup, D. E., R. E. Carlson, and R. T. Heath. 2003. The effect of predation risk and foraging return on the diel use of vegetated habitat by two size classes of bluegill (*Lepomis macrochirus*). Transactions of the American Fisheries Society 132:590–597.
- Shoup, D. E., and D. H. Wahl. 2009. The effect of turbidity on

360

prey selection by largemouth bass. Transactions of the American Fisheries Society 138:1018–1027.

- Stein, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology 58:1237–1253.
- Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. Ecology 57:751–761.
- Steinhart, G. B., R. A. Stein, and E. A. Marschall. 2004. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? Journal of Great Lakes Research 30:381–389.
- Sweka, J. A., and K. J. Hartman. 2003. Reduction of reactive distance and foraging success in smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. Environmental Biology of Fishes 67:341–347.
- Tester, A. L. 1932. Food of the small-mouthed black bass (*Micropterus dolomieu*) in some Ontario waters. University of Toronto Studies, Biological Series.
- Vandenbyllaardt, L., F. J. Ward, C. R. Braekevelt, and D. B. McIntyre. 1991. Relationships between turbidity, piscivory, and development of the retina in juvenile walleyes. Transactions of the American Fisheries Society 120:382– 390.

- Vinyard, G. L., and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). Journal of the Fisheries Research Board of Canada 33:2845–2849.
- Wahl, D. H. 1995. Effect of habitat selection and behavior on vulnerability to predation of introduced fish. Canadian Journal of Fisheries and Aquatic Sciences 52:2312–2319.
- Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society 117:142– 151.
- Weidel, B. C., D. C. Josephson, and C. C. Krueger. 2000. Diet and prey selection of naturalized smallmouth bass in an oligotrophic Adirondack lake. Journal of Freshwater Ecology 15:411–417.
- Winemiller, K. O., and D. H. Taylor. 1987. Predatory behavior and competition among laboratory-housed largemouth and smallmouth bass. American Midland Naturalist 117:148–166.
- Wray, W. J., and L. D. Corkum. 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research 27:329–334.